# THE ANATOMY AND TAXONOMY OF *VANCLEVEA* (ASTERACEAE)[1]

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Abstract.— Wood, leaf, and floral anatomy of *Vanclevea stylosa* is compared with that of several possibly related species in the genera *Acamptopappus*, *Eastwoodia*, *Grindelia*, *Haplopappus*, and *Petradoria*. Although *V. stylosa* was originally described as a *Grindelia*, it is clearly distinct from that genus. Of the taxa studied, it is most closely allied to *Haplopappus salincinus* and *H. scopulorum*. The taxonomy, morphology, and distribution of the monotypic *Vanclevea* are detailed, and known exsiccatae are listed.

Eastwood (1896) published the species *Grindelia stylosa* and noted, "It differs from typical *Grindeliae* in having entire leaves, turbinate involucres, and more numerous persistent pappus bristles. The long, conspicuous styles give to the flower its chief beauty, hence the name." A few years later, Greene (1899) made the species the basis of his genus *Vanclevea*. Steyermark (1937) stated,

> *Vanclevea* is closely related to *Grindelia* by its resinous involucres and pappus of comparatively few (12 or so) bristles, but differs in having a persistent pappus of more numerous bristles, very elongated exserted style branches and appendages, leaves of entirely different insertion and position, as well as a peculiar shedding epidermis of the stem. *Vanclevea* appears to be more closely related to *Acamptopappus* and is also related to *Chrysothamnus*.

The senior author's interest in the latter genus and related Astereae prompted the present study of this little-known monotypic genus. One of the closest morphotypes is *Petradoria discoidea*, formerly known as *Chrysothamnus gramineus* (cf. Anderson, 1963).

## Methods and Materials

Fresh and dried materials were processed for anatomical study as in earlier studies (Anderson, 1963, 1970a). Generally, the basal portion of the central stem was used for study of wood features, but in *Grindelia decumbens* a portion of the upper root was used. Five heads from personal collections, along with two heads from other collections, were measured (as in Anderson, 1964) for involucral and floral data.

Taxa morphologically similar to *Vanclevea* plus some taxa previously considered related to that genus are included in the study. Specific voucher specimens are: *Acamptopappus schockleyi* Gray, *Anderson 2120* (KSC); *A. sphaerocephalus* (Harv. & Gray) Gray, *Anderson 2110*, *2112* (KSC); *Eastwoodia elegans* Bdg., *Eastwood 5838* (KSC); *Grindelia columbiana* (Piper) Rydb., *Anderson 3591* (KSC); *G. decumbens* Greene, *Anderson 2678* (KSC); *G. squarrosa*

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(Pursh) Dunal., *Anderson 3117, 3529* (KSC); *G. squarrosa* var. *nuda* (Wood) Gray, *Anderson 2986* (KSC); *Haplopappus salicinus* Blake, *Eastwood 10* (US); *H. scopulorum* (Jones) Blake, *Anderson 2145* (KSC); and *Vanclevea stylosa* (Eastw.) Greene, *Anderson 1976, 3156, 3337* (KSC).

## Anatomy

Seedling data are limited. *Vanclevea* seedlings have opposite leaves, a feature shared with *Chrysothamnus* and woody *Haplopappus* such as *H. scopulorum;* those of *Grindelia* are alternate.

Adult leaves of *Vanclevea* are isolateral with massive sclerenchymatous bundle sheaths and heavy cuticle (10-13$\mu$). The leaves are essentially glabrous; however, a few small glandular trichomes occur at the leaf base. The most similar leaves (isolateral with massive sclerenchyma bundle sheaths) are found in *H. salicinus* and *H. scopulorum;* but the former has glandular hairs sparsely distributed on both leaf surfaces, and the latter has nonglandular hairs adaxially. Leaves of *Petradoria* (Anderson, 1963) are also somewhat similar to those of *Vanclevea. Acamptopappus* leaves are isolateral but have little or no sclerenchyma in the bundle sheaths; *A. shockleyi* leaves have uniseriate, nonglandular trichomes, whereas those of *A. sphaerocephalus* are glabrous. Leaves of *Eastwoodia* are isolateral, have glandular hairs along the midvein adaxially, and lack sclerenchyma in the bundle sheaths. Leaf anatomy in our *Grindelia* agrees with that of earlier studies (Dalbey, 1914; Giroux and Susplugas, 1935). *Grindelia* is unlike the other genera in that the leaves have prominent bundle-sheath extensions with little or no sclerenchyma associated with the veins. The epidermis is glandular-pitted with short multiseriate trichomes, and the mesophyll is isolateral to weakly bifacial.

Stems of *Vanclevea* are weakly pentagonal in transection just below the nodes but tend to be cylindrical farther below the nodes. The cortex has large collenchyma strands associated with the five ridges of the stem. The collenchyma strands are separated by zones of parenchyma. The endodermis does not contain casparian strip and is poorly defined in young stems; it becomes more prominent with age as the cork cambium is initiated deep in the cortex next to the endodermis. The endodermis is the only row of cells separating the cork and cork cambium from the extensive phloem fibers that cap the vascular bundles. The cork cambium is precocious, being activated simultaneously with the vascular cambium. The deep-seated origin of the periderm in *Vanclevea* stems accounts for the "peculiar shedding epidermis" noted by Steyermark (1937). Cells of the pith become thick-walled through secondary sclerosis.

Collenchyma distribution in stems of the other taxa studied is basically similar to that of *Vanclevea*, although it is not so extensive. Furthermore, in *Acamptopappus* species, the collenchyma forms a continuous band, two to three cells thick, around the stem rather than being separated by groups of parenchyma. Cork initiation in *Eastwoodia* and *H. scopulorum* is also deep in the cortex; however,

four to five cell layers of parenchyma separate the cork cambium from the phloem fibers. Also, the periderm formation lags well behind the secondary vascular growth.

*Vanclevea* is the woodiest shrub of the taxa studied, with stems occasionally measuring up to 8 cm in diameter; the *Grindelia* species are the least woody. Selected features of woody anatomy are listed in Table 1. For comparisons with other related members of the Astereae, consult Carlquist (1960) and Anderson (1963, 1972). Measurements taken from a twig of *Eastwoodia elegans* were too limited to include in the table; the species has narrow vessel elements (about 30$\mu$ wide and 136$\mu$ long) and small wood rays about 0.7 mm tall.

The largest vessel elements and libriform fibers occur in the *Haplopappus*, followed closely by *Acamptopappus* and *Vanclevea* with *Grindelia* having relatively narrower and shorter xylem cells. The pattern of vessel grouping varies. In *Grindelia*, vessels are in single files (radial chains); those of *Vanclevea* are in groups a few cells wide but still somewhat radially aligned. Vessels in *Acamptopappus* and *H. scopulorum* are in larger, tangentially clustered groups. All woods tend to be diffuse-porous, but in *Vanclevea* they are semi-ring-porous. Although most woods tend to have wider vessels in the springwood and narrower ones in the summerwood, vessels in *A. sphaerocephalus* are widest in the mid-season wood of each ring, as in *H. acaulis* (Anderson, 1963).

Vascular tracheids are present but not common in *Vanclevea* woods. They are abundant and storied in wood of *H. scopulorum*. Axial parenchyma is paratracheal and scanty in most samples; in *Grindelia* species, paratracheal parenchyma is more abundant. That plus the taller, wider wood rays probably relate to the herbaceous nature of *Grindelia*. *Eastwoodia* and *Grindelia* also have a few uniseriate rays in their woods.

Paedomorphosis is clearly demonstrated in the patterns of change in vessel-element length during growth in the *Grindelia* taxa; the other taxa have a "normal or woody" growth curve (see Anderson, 1972).

Floral development in *Vanclevea* follows a common pattern in Astereae (Martin, 1892; Anderson, 1970a); floral organs are initiated in the sequence: corolla, stamens, pappus, and carpels. The species develops a Polygonum-type embryo sac. Mature embryo sacs (310-360$\mu$ long and 22-25$\mu$ wide) have three antipodals. There are no multinucleate antipodals, nor is there the increase in antipodal number beyond three that frequently occurs in related Astereae. The long, narrow embryo sacs resemble those in certain *Chrysothamnus* taxa (Anderson, 1970b). Embryo sacs seen in *Haplopappus scopulorum* were 160$\mu$ long and also contain three antipodals. Embryo sacs in *Grindelia squarrosa* have only two antipodals, with one or both developing prominent lateral haustoria (Howe, 1926). Embryo sacs in our material of *G. decumbens* and *G. squarrosa* var. *nuda* also have two antipodals with lateral haustoria, apparently the basic pattern in *Grindelia*.

TABLE 1. Comparative xylary features of *Vanclevea* and other Astereae.

| Taxon and collection | Vessel elements | | | Libriform fibers | | | Multiseriate rays | | |
|---|---|---|---|---|---|---|---|---|---|
| | Widest diameter, μ | Average diameter, μ | Average length, μ | Average diameter, μ | Average length, μ | Average height, mm | Average cell number at maximum width | Cells isodiametric to procumbent* | Cells isodiametric to erect |
| *Acamptopappus sphaerocephalus, Anderson 2112* | 90.8 | 50.7 | 147.9 | 17.4 | 212.2 | 2.09 | 3.4 | + | – |
| *Grindelia decumbens, Anderson 2678* | 56.8 | 34.2 | 120.0 | 12.6 | 201.6 | 2.11 | 12.6 | 0 | + |
| *G. squarrosa, Anderson 3117* | 64.0 | 38.7 | 112.0 | 12.8 | 159.7 | 1.58 | 10.2 | + | + |
| *G. squarrosa* var. *nuda, Anderson 2986* | 78.4 | 40.9 | 127.3 | 14.6 | 212.0 | 1.19 | 4.7 | – | + |
| *Haplopappus scopulorum, Anderson 2145* | 97.6 | 69.5 | 156.1 | 17.2 | 249.7 | 1.13 | 3.1 | + | – |
| *Vanclevea stylosa, Anderson 1976* | 84.8 | 47.2 | 142.9 | 15.3 | 224.3 | 1.31 | 4.6 | + | + |
| *Anderson 3156* | 87.4 | 43.6 | 151.2 | 15.4 | 212.4 | 1.90 | 4.4 | + | – |

* + = frequent, – = infrequent, 0 = absent

Aspects of *Vanclevea* floral morphology are listed in Table 2. The heads are always discoid. Flower numbers (from single head counts) in our other taxa include: *Acamptopappus schockleyi*, 12 ray and 54 disc flowers; *A. sphaerocephalus*, 22 disc; *Eastwoodia elegans*, 50 disc; *Grindelia decumbens*, 12 ray and 59 disc; *G. squarrosa*, 38 ray and 270 disc; *G. squarrosa* var. *nuda*, 222 disc; *Haplopappus salicinus*, 12 disc; and *H. scopulorum*, 9 disc in ours and 24 in *Eastwood & Howell 7111* (RSA).

Differences in pappus are frequently considered characteristics for distinguishing genera in the Asteraceae. Among species under study, extremes are seen between *Grindelia* and *Haplopappus*. The former has two to eight deciduous, paleacous awns, whereas the latter has numerous persistent, capillary bristles. Pappus of *Vanclevea* is somewhat intermediate, though more like the *Grindelia* in having 15-18 tardily deciduous, paleacous awns. However, one *Vanclevea* flower from *Holmgren & Hansen 3801* was found with a small gall (chalcid-fly induced) arising from the top of the achene beside the corolla. (The senior author has found similar galls occasionally in *Chrysothamnus* and *Haplopappus*.) The pappus adjacent to the gall is composed of numerous capillary bristles 6 mm long, whereas the pappus adjacent to the corolla is typical, consisting of eight paleacous awns each about 2.5 mm long. Perhaps too much significance is attached to pappus differences in the Asteraceae. Shinners (1949) certainly thought so.

Data on floral anatomy are presented in Table 3; the format follows that in Anderson (1970a). Frequency classes are: ++, abundant; +, frequent; –, rare; and 0, absent. Zones I and II are the proximal and distal areas of the achene, respectively; zones III - V are from the corolla; and VI and VII, from the style. Trichome types d, n, and g are duplex (the nonglandular twin-hairs characteristic of achenes), uniseriate nonglandular, and biseriate glandular, respectively. Corolla thickness (cell number) was determined at

TABLE 2. Features of floral morphology in *Vanclevea stylosa*

| Collection | Bract number | Involucral length, mm | Involucral width, mm | Flower number | Flower length, mm | Corolla lobe length, mm | Style length, mm | Stigmatic area—total style branch, % |
|---|---|---|---|---|---|---|---|---|
| *Anderson 3156* | 55.6 | 12.0 | 6.9 | 44.2 | 7.8 | 1.0 | 13.5 | 42.2 |
| *Anderson 3337* | 51.0 | 10.5 | 7.5 | 43.6 | 7.3 | 1.0 | 11.6 | 41.8 |
| *Eastwood & Howell 6660* | 46.5 | 12.4 | 6.9 | 34.0 | 8.2 | 0.9 | 13.6 | 43.5 |
| *Cutler 3155* | 66.0 | 10.0 | 7.5 | 36.5 | 8.0 | 1.2 | 13.2 | 45.8 |
| *Holmgren & Hansen 3801* | 45.5 | 11.9 | 7.2 | 32.0 | 7.4 | 1.2 | 11.4 | 35.9 |

TABLE 3. Selected features of floral anatomy in *Vanclevea* and other Astereae.

| Taxon | Ovarian bundle number | | Secretory canal distribution | | | | | | | Trichomes | | | | | | Disc corolla thickness (cell number) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Achene | | Corolla | | | Style | | Achene | | | Corolla tube | | | | | |
| | Average | Range | I | II | III | IV | V | VI | VII | Type | Frequency | Length, μ | Type | Frequency | Length, μ | A | B | C |
| *Acamptopappus schokleyi* | 8.6 | 8-10 | ++ | ++ | 0 | 0 | 0 | 0 | 0 | d | ++ | 1000 | g | + | 100 | 8 | 5 | 2 |
| | | | | | | | | | | n | ++ | 1000 | | | | | | |
| *A. sphaerocephalus* | 9.0 | 8-10 | ++ | ++ | 0 | 0 | 0 | 0 | 0 | d | +++ | 1100 | g | ++ | 200 | 10 | 6 | 2 |
| | | | | | | | | | | n | ++ | 1200 | | | | | | |
| *Eastwoodia elegans* | 5.0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | d | + | 300 | 0 | | | 8 | 6 | 2 |
| *Grindelia decumbens* | 2.0 | 2 | 0 | 0 | – | ++ | ++ | ++ | ++ | 0 | | | 0 | | | 8 | 6 | 2 |
| *G. squarrosa* | 2.0 | 2 | 0 | 0 | ++ | ++ | ++ | ++ | ++ | g | – | 40 | 0 | | | 9 | 6 | 2 |
| *G. squarrosa* var. *nuda* | 2.0 | 2 | 0 | 0 | + | ++ | ++ | ++ | ++ | 0 | | | 0 | | | 9 | 6 | 2 |
| *Haplopappus salicinus* | 5.2 | 5-6 | + | ++ | 0 | – | + | 0 | 0 | d | + | 400 | 0 | | | 8 | 6 | 2 |
| *H. scopulorum* | 8.3 | 7-9 | 0 | + | + | ++ | ++ | 0 | 0 | d | ++ | 400 | 0 | | | 9 | 6 | 2 |
| *Vanclevea stylosa* | | | | | | | | | | | | | | | | | | |
| *Anderson 1976* | 6.2 | 5-7 | – | + | 0 | + | + | 0 | 0 | d | + | 400 | 0 | | | 11 | 5 | 2 |
| *Anderson 3156* | 6.9 | 6-8 | – | + | + | ++ | ++ | 0 | 0 | d | – | 380 | 0 | | | 12 | 6 | 2 |
| *Anderson 3337* | 5.8 | 5-7 | 0 | + | 0 | + | ++ | 0 | 0 | d | – | 270 | 0 | | | 11 | 6 | 2 |

three levels; those levels (A-C) and the seven zones studied for secretory canals are diagrammatically shown in Fig. 24 of Anderson (1970a).

Data relating to ray flowers are not included in Table 3 because several of the taxa are eradiate. Ray flowers of *Grindelia decumbens* have short (90$\mu$), biseriate glandular trichomes, though none are found on the disc flowers. Trichomes in *Acamptopappus* are distinctive. Long isotropic, nonglandular trichomes (shag hairs) are found abundantly with the anisotropic duplex hairs on the achene walls. Duplex hairs were found only distally on *Vanclevea* achenes, and in *Grindelia squarrosa* the rare glandular hairs are restricted to the very top of the otherwise glabrous achenes.

Ovarian vascular bundle number and the pattern of secretory canal distribution (present in achenes and corollas but absent in styles) are similar in the *Haplopappus* and *Vanclevea*. At least a few flowers of all samples from those two genera have additional corolla vasculature (midveins); the other taxa had only five veins in their disc corollas. *Grindelia* is set apart from the other taxa by its highly reduced vasculature in the achenes.

Xeromorphy in *Vanclevea* flowers is evidenced in the thickness of its corollas and the massive sclerenchyma sheaths that surround the veins in the achenes.

## Taxonomy

Although *Vanclevea stylosa* was first described as a *Grindelia*, that relationship apparently is not close. In addition to having features of habit, morphology, and anatomy presented here, the two groups are distinguishable chromosomally. In *Grindelia*, $x = 6$, whereas the single documented count for *Vanclevea* is $n = 9$ (*Anderson 1976* in Solbrig et al., 1964). The remaining taxa studied here are also $n = 9$ or chromosomally unknown, as in *H. salicinus*.

The purported relationships of *Vanclevea* to *Acamptopappus* and *Chrysothamnus* (Styermark, 1937) now do not appear close. The genus has many features in common with *Haplopappus salicinus* and *H. scopulorum*. It is with that section of *Haplopappus* (*Hesperodoria*) that *Vanclevea* is most closely allied. Although pappus in *H. ciliatus* (section *Prionopsis*) more than in any other *Haplopappus* resembles that of *Vanclevea*, *H. ciliatus* differs from *Vanclevea* in most other features of morphology, anatomy, and cytology. *Haplopappus* (*sens. lat.*) is badly in need of revision, but we believe that after such a study, *Vanclevea* will still be considered a separate genus in the Astereae.

*Vanclevea* Greene, Pittonia 4:50. 1899.

E. L. Greene dedicated this monotypic genus to a Mr. J. W. Van Cleve of Dayton, Ohio.

*Vanclevea stylosa* (Eastw.) Greene, Pittonia 4:51. 1899.

Basionym: *Grindelia stylosa* Eastw., Proc. Calif. Acad. Sci. II 6:293. 1896.

TYPE: [Epsom Creek] Barton's Range, San Juan Co., Utah, 13 July 1895, *A. Eastwood* 36. CAS (holotype) US!, photo - KSC!

Slender branching shrubs (4) 6-7 (10) dm tall, older stems with shedding epidermis or dull white bark, often with axillary fascicles of small leaves, younger stems greenish white, glutinous, glabrous; leaves alternate, linear lanceolate, rigid, spreading to falcate and recurved, occasionally conduplicate, entire, (2.5) 3-3.5 (4.5) cm long and (2.5) 3-4 (5) mm wide; inflorescence cymose or a solitary head, discoid, viscous; involucres broadly turbinate, (9.5) 10-12 (12.5) mm tall, bracts graduated, subulate to broadly linear, acute to acuminate, often squarrose; flowers (31) 35-45 (48); corollas yellow, 7-8.5 mm long, lobes usually 1 mm long; styles well exerted, appendages longer than stigmatic lines; pappus of (12) 15-18 paleacous awns, stramineous, 2.5-3 mm long, often exceeding the involucre at anthesis; achenes narrowly cylindric, 4-5 mm long, nearly glabrous. $n = 9$.

Variation within the species is not great, and no subspecific taxa are recognized. In most plants the bracts are squarrose and acuminate to apiculate, but some are ascending and only acute. The degree to which the pappus is visible at anthesis also varies.

DISTRIBUTION: Sandy washes and sand hills; from Emery and Grand counties south through the Canyonlands Section of Utah to Coconino and Navajo counties in Arizona (Fig. 1).

PHENOLOGY: Primarily blooming July through September, but occasionally later in the autumn and in March.

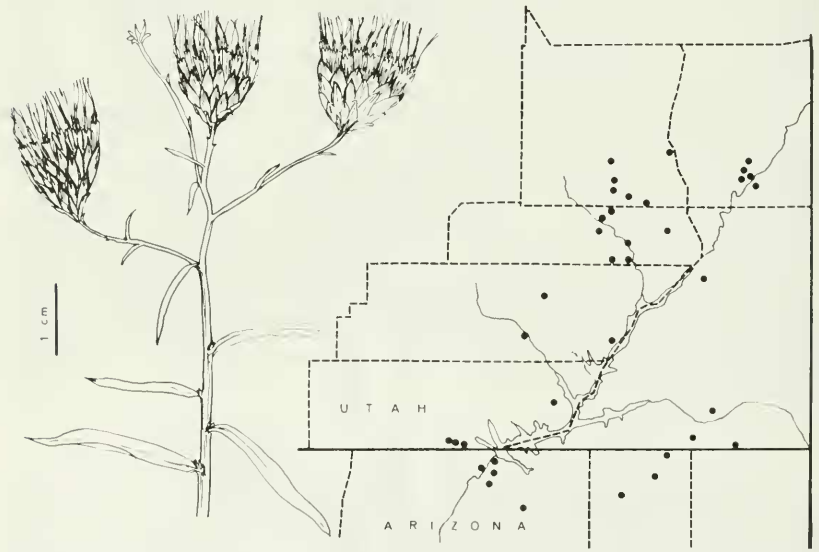


Fig. 1. Flowering twig of *Vanclevea stylosa* and the known distribution of the species.

Exsiccatae: ARIZONA. Coconino Co.: Page, elev. 4300 ft, *L. C. Anderson 1976* (KSC); 11 mi SSW Page, elev. 5100 ft, *L. C. Anderson 1715* (UC, NY, RSA), *2619* (KSC); 9.3 mi SSW Page, *N. D. Atwood, S. L. Welsh, & B. Wood 3339* (BRY); 6 mi SW Page, elev. 4500 ft, *J. Daney* in 1971 (ASC), *R. H. Hevly & J. States* in 1972 (ASC); 1.5 mi below Lee's Ferry, *H. C. Cutler 3155* (MO, NY, US, SMU); Kaibito Plateau, elev. 6000 ft, *L. D. Love* in 1934 (ARIZ). Navaja Co.: Monument Valley, *A. Eastwood & J. T. Howell 6660* (CAS, UC, US), *J. T. Howell & G. True 44882* (CAS), *E. McClintock* in 1963 (CAS), *M. Blas 38* (CAS); 7 mi SW Utah line toward Kayenta, elev. 5400 ft, *J. T. Howell & G. True 45018* (CAS, NY); Tsegi Canyon, *L. C. Whitehead* in 1916 (ARIZ). UTAH. Emery Co.: Temple Wash, T25S, R11E NW¼ Sec 12, *L. C. Anderson 3337* (KSC); 2 mi E Gilson Butte, Green River Desert, elev. 4800 ft. *A. Baker 5* (US); Andy Moore North Spring [T26S, R15E], San Rafael Desert, elev. 5000 ft, *Bryan & Read* in 1938 (UTC); 5 mi E Jeffrey Well, Green River Desert, elev. 4500 ft, *W. P. Cottam 17761* (COLO, UT); W Robber's Roost, *L. A. Stoddart* in 1943 (UTC); Dry Lake Wash, ca. 15 mi S Green River, *S. L. Welsh, N. D. Atwood, & G. Moore 10833a* (BRY, NY). Garfield Co.: 18 mi E Boulder vic. Circle Cliffs, *B. Maguire* in 1940 (NY); Baker's Ranch [T37S, R7E], *B. Markham* in 1940 (UTC); *Ticebo Mesa*, T36S, R12E, *J. C. Pederson 26* (BRY). Grand Co.: S Double Arch, Arches Nat'l Monument, *L. C. Anderson 66* (UTC); Courthouse Towers, Arches Nat'l Monument, *S. L. Welsh, B. F. Harrison, & G. Moore 2268* (BRY); S Turnbow Cabin, Salt Wash, Arches Nat'l Monument, *S. L. Welsh & G. Moore 2717* (BRY, NY); Little Sand Flats, E Moab, elev. 4500 ft, *K. Goodspeed* in 1968 (UTC). Kane Co.: 2.5 mi W Glen Canyon City, *L. C. Anderson 3156* (KSC); 2 mi E Glen Canyon City, *N. D. Atwood 3095* (BRY); 6 mi E Glen Canyon City, *N. D. Atwood & D. Kaneko* (UT); Fiftymile spring S Escalante [T40S, R8E], *J. R. Murdock 375* (BRY); 55 mi E Kanab, *S. L. Welsh 9418* (BRY). San Juan Co.: Forbidding Canyon, Rainbow Bridge area, elev. 3600 ft, *R. A. Darrow 2806* (ARIZ); Monument Valley, *A. Eastwood & J. T. Howell 6675* (CAS, K, NY, UC); S. Needle Rock, Monument Valley, *A. H. Holmgren & S. Hansen 3801* (NY, UC, US, UTC); Lower Beef Basin [T32S, R8E], NW Monticello, *W. A. Shands 140* (US); N Mexican Water, elev. 4900 ft, *B. Smith* in 1966 (UTC). Wayne Co.: 20 mi N Hanksville, *R. Jensen* in 1941 (UTC); Burr Point [T30S, R13E], *B. Markham* in 1940 (UTC); SSE Hanksville near county line, *W. A. Shands 124* (US); 2 mi E Wadlerman Home, S Hanksville, *W. A. Shands 140* (UT); San Rafael Desert, elev. 4500 ft, *W. D. Stanton 1068* (UT); Barrier (Horseshoe) Canyon, *S. L. Welsh, N. D. Atwood, & G. Moore 10867* (BRY, NY); 5 mi N Hanksville, *S. L. Welsh & G. Moore 3614* (BRY).

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